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Effects of human land use and temperature on community dynamics in European forests

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ABSTRACT

Climate change and human land use are thought to play a dominant role in the dynamics of European central-latitude forests in the Holocene. A wide range of mathematical and statistical models have been used to study the effects of these variables on forest dynamics, including physiologically-based simulations and phenomenological community models. However, for statistical analysis of pollen count data, compositional data analysis is particularly well suited, because pollen counts give only relative information. We studied the effects of changes in human land use and temperature on European central-latitude forest dynamics at 7 sites over most of the last 10ka, using a stochastic model for compositional dynamics of pollen count data. Our approach has a natural ecological interpretation in terms of relative proportional population growth rates, and does not require information on pollen production, dispersal, or deposition. We showed that the relative proportional population growth rates of *Fagus* and *Picea* were positively affected by intensified human land use, and that those of *Tilia* and *Ulmus* were negatively affected. Also, the relative proportional population growth rate of *Fagus* was negatively affected by increases in temperature above about 18°C. Overall, the effects of temperature on the rate of change of forest composition were more important than those of human land use. Although there were aspects of dynamics, such as short-term oscillations, that our model did not capture, our approach is broadly applicable and founded on ecological principles, and gave results consistent with current thinking.

1. Introduction

Drivers of forest dynamics include succession following disturbance by fire, pathogens or storm damage (Seidl et al., 2011), the clearance and use of forests by people, particularly as forage for livestock (Bradshaw and Mitchell, 1999) and the effects of climate change on forest composition and migration of trees (Iversen, 1960; Giesecke et al., 2017). Forest dynamics can be directly observed and monitored using permanent plots (Tinkham et al., 2018) or remote sensing (European Environment Agency, 2017), but these approaches only cover recent decades, while individual trees can live for several centuries. Palaeoecological analyses including palynology and dendrochronology can extend the timescale of analyses of forest dynamics, although these data sources are less precise than direct observation (Brewer et al., 2012). Such longer-term analyses have emphasised the dominant role of climate change and human land use on European temperate and boreal forest dynamics (Marquer et al., 2017). Much of Europe was quickly reforested in response to rapid warming following the last glaciation, and the culmination of the spread of deciduous forests into Scandinavia occurred in the mid-Holocene, reflecting the increasing warmth of the growing season. The late Holocene was characterised by a steady decline in treeline altitude in northern Europe and an expansion of peatland area as climate became cooler and wetter (Giesecke et al., 2017). Europe was primarily a forested continent prior to the spread of Neolithic agriculture, but temperate forest cover declined during the last 6ka through progressive fragmentation, primarily as a result of clearance for arable and pastoral land (Roberts et al., 2018).

Reconstructions of past climate and human land use are needed to determine the effects of these variables on long-term forest dynamics. The reconstruction of Holocene climate has been based

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on many different physical, geochemical and biological proxy systems, often involving a transfer function approach (e.g. Webb and Bryson, 1972; Juggins and Birks, 2012). Climate models have also been run for specific periods of the Holocene (e.g. Bakker et al., 2014; Zhang et al., 2018), but all methods of palaeoclimate reconstruction incorporate high degrees of uncertainty and reflect inherent spatial variation. Our understanding of the Holocene development of land use is founded on collaborative research between archaeologists, palynologists and ecologists, which has been integrated into an empirically-grounded global summary (Stephens et al., 2019). For numerical modelling, the History Database of the Global Environment (HYDE: Klein Goldewijk et al., 2017) and the KK10 reconstruction (Kaplan et al., 2011) have been frequently used.

Early studies explored the influence of climate alone on Holocene forest dynamics. For example, comparison of pollen records with climate-driven dynamic forest models showed that climate affected interspecific competition (Lischke et al., 2002) and northern distribution limits of tree taxa (Miller et al., 2008). More recent studies have estimated the relative importance of both climate and human land use on pollen records using variance partitioning. For example, climate was more important than human land use in explaining variability in forest composition in Estonia during the late Holocene (Reitalu et al., 2013), and climate was the main driver of changes in Holocene boreal forest composition at the regional scale (Kuosmanen et al., 2016). Recent comparisons using dynamic vegetation modelling tell a similar but more nuanced story. For example, in northern and western Europe, climate was the strongest driver of Holocene vegetation dynamics until 2ka BP, after which time climate and land use were both significant factors (Marquer et al., 2017).

Questions about the effects of human land use and climate on forest dynamics can be answered using a range of mathematical and statistical models. In physiologically-based static equilibrium models such as STASH (Sykes et al., 1996), bioclimatic variables including growing degree days and drought tolerance are used to predict potential species distributions under given climate scenarios. In physiologically-based dynamic models such as FORSKA (Prentice and Leemans, 1990) and LPJ-GUESS (Smith et al., 2001), processes such as regeneration, growth and mortality are modelled using systems of equations derived from a mixture of basic physical principles and empirical biological rules. Vegetation dynamics can be simulated and compared with observations, once the models are parameterised and climatic variables are provided. Alternatively, phenomenological models at the community level can be fitted to time series of observations. The Lotka-Volterra model is the most widely-used such model, mainly because it is the simplest plausible approximation to potentially very complicated interspecific interactions (Lotka, 1956, p. 60). Lotka-Volterra modelling of pollen accumulation data for pairs of tree taxa suggests that interspecific interactions were more important than temperature or nitrogen in determining forest dynamics at a site in Scotland (Jeffers et al., 2015).

Different approaches are needed for pollen count data. In such data, the total number of pollen grains per unit volume of sediment depends on factors such as vegetation area (Mosimann, 1962) and sedimentation rate (Mosimann, 1963). Pollen analysts therefore typically count a fixed number of pollen grains from the sample for a given site and time (Berglund and Ralska-Jasiewiczowa, 1986, p. 462), and it is the proportions of pollen types counted, rather than their total, that give information about vegetation composition. Thus, either pollen proportions must be converted into estimates of plant abundance using external information and a mathematical model such as REVEALS (Sugita, 2007), or inferences must be made directly from pollen proportions. In the latter approach, all sets of counts with the same pollen proportions should usually be treated as being equivalent. This is the fundamental principle of compositional data analysis (Pawlowsky-Glahn et al., 2015, p. 9). In compositional data analysis, all the relevant information about a system is contained in sets of logs of ratios of relative abundances (Aitchison, 1986, chapter 4). Thus, models for the dynamics of these logs of ratios (i.e. models for compositional dynamics) are a natural approach to the study of forest dynamics using pollen proportions.

Here, we study the effects of changes in human land use and temperature on European central-latitude forest dynamics over most of the last 10ka, using a stochastic model for compositional dynamics and time series of Holocene pollen count data from multiple sites. We estimate effects of human land use and temperature on the relative proportional population growth rates of individual taxa, and the pollen proportions that would have been expected if human land use and temperature had remained constant. We also determine whether human land use or temperature had larger effects on the rate of change of forest composition, for each site and each time point.

2. Methods

2.1. Pollen data

Pollen data from the European Pollen Database (EPD: European Pollen Database, 2018) were obtained from seven extant lakes or former lake sites with sediment profiles covering at least most of the last 10ka, and which had been dated using at least 12 radiocarbon dates or varve chronology (Table 1). All sites other than Hockham Mere had the most recent pollen data less than 0.5ka BP (for Hockham Mere, the most recent pollen data were from 1.510ka BP). The sites are located throughout central latitudes in Europe and all possess a diverse pollen flora derived from the major tree taxa that were present. We did not include Scandinavian sites as their tree flora is less diverse than that at lower latitudes (Svenning et al., 2010). We did not include sites at latitudes below 45°N as forest composition there can diverge significantly from central latitudes (Binney et al., 2017). Pollen analyses mostly comprised several hundred pollen samples with large pollen counts. We included only those pollen samples taken between 10ka BP and 100a BP, when forest was the predominant vegetation type in our study area (Berglund et al., 1996): furthermore, the land use data described below end at 100a BP. We chose to use pollen data from ten tree taxa (*Alnus*, *Betula*, *Corylus*, *Fagus*, *Fraxinus*, *Picea*, *Pinus*, *Quercus*, *Tilia* and *Ulmus*) as these pollen types dominate the tree pollen record in the study area and include pollen from the major tree species that have occurred in European central-latitude forests since the last glaciation (Giesecke et al., 2017). Our focus is on modelling the relative dynamics of these tree taxa within remaining forested areas. Exclusion of minor trees, Poaceae and other non-arboreal taxa, required to reduce computational effort, does not affect these relative dynamics, but it is important to remember that our results reflect dynamics within this subset, not within all plant taxa and the inferred landscape vegetation. We used dates based on models relating depth of sediment to calendar age (Giesecke et al., 2014) at all sites except for Holzmaar, for which we used author-preferred dates from the EPD based on annual laminations (Kubitz, 2000).

2.2. True dynamics of relative abundances

We model the dynamics of relative abundances using a stochastic differential equation, with a deterministic component

Table 1
Site details. Altitude is in m Above Mean Sea Level (AMSL). Time points is the number of time points included in the analysis, between 10ka BP and 100a BP, not the number in the original data set. The time range is from the oldest to the youngest time point included in the analysis (all original data sets had time points older than the oldest included, and some had time points younger than the youngest included). Pollen counts are totals for the taxa of interest over the time points included in the analysis. Number of dates is the number of radiocarbon dates or annual laminations (varves) used to date the observations. Sources: Hockham Mere, Bennett (1983); Holzmaar, Litt et al. (1997); Meefelder Maar, Kubitz (2000); Lake Gościaż, Ralska-Jasiewiczowa et al. (1998); Lavpicco, Finsinger and Tinner (2006); Lobsigensee, Ammann (1985); Preluca, Feurdean (2005).

Site	Country	Lat/Long	Altitude/m AMSL	Time points [time range/ka BP]	Pollen count median [range]	Number of dates
Hockham Mere	UK	N52°29'32.17"W0°51'1.48"	33	111 [9.972, 1.510]	1040 [458, 1408]	23 (^{14}C)
Holzmaar	Germany	N50°07'09.02"E6°52'43.21"	425	75 [9.810, 0.101]	942 [332, 234]	85 (annual laminations)
Lake Gościaż	Poland	N52°34'58.21"E19°20'22.40"	64	181 [9.966, 0.110]	1249 [297, 2779]	278 (annual laminations)
Lavpicco	Italy	N45°03'16.38"E07°23'31.03"	356	258 [9.990, 0.323]	353 [66, 882]	12 (^{14}C)
Lobsigensee	Switzerland	N47°01'50.01"E7°17'53.22"	514	105 [9.930, 0.446]	956 [250, 1786]	32 (^{14}C)
Meerfelder Maar	Germany	N50°06'02.95"E6°45'27.05"	336	385 [9.967, 0.163]	1015 [318, 1258]	406 (annual laminations)
Preluca	Romania	N47°19'05.13"E23°32'18.35"	730	133 [9.942, 0.108]	389 [174, 635]	14 (^{14}C)

describing the effects of biological processes and climate, and a stochastic component describing random variability in continuous time. We need a stochastic model because it is likely that forest dynamics are affected by events that are difficult to predict, such as short-term environmental fluctuations. We need a continuous-time model because the pollen observations are not equally spaced in time. These two considerations make a stochastic differential equation (e.g. Higham, 2001; Dennis and Ponciano, 2014) appropriate. Our model is the continuous-time analogue of the discrete-time vector autoregressive models widely used for studying community dynamics (e.g. Ives et al., 2003; Hampton et al., 2013). Vector autoregressive models for communities often use log-transformed abundances, which lead to the multivariate equivalent of the stochastic Gompertz model for population dynamics (Ives et al., 2003). This is not appropriate for relative abundances, which are constrained to sum to 1. Instead, we follow a compositional data analysis approach, using the isometric logratio (ilr) transformation (Egozcue et al., 2003) to map a set of $s+1$ tree relative abundances $\mathbf{y}_i(t)$ at site i, time t (usually in terms of total basal area) to a set of s unconstrained real numbers $\mathbf{x}_i(t)$ (supporting information, section S1). Similar transformations have previously been used in vector autoregressive models of coral reef dynamics, where relative abundances are measured as proportions of space covered by each group of organisms (Cooper et al., 2015; Gross and Edmunds, 2015; Allen et al., 2017). This transformation is applied to unobserved tree relative abundances, which are assumed to lie strictly in the open standard s-simplex, and are therefore never zero. Pollen values are assumed to arise by multinomial sampling from the tree relative abundances, as described below. Thus, zero pollen values do not require any special treatment.

We assume that the dynamics of $\mathbf{x}_i$ can be described by the stochastic differential equation

$$\mathrm{d}\mathbf{x}_i(t) = \left(\mathbf{a}_i + \mathbf{c}q_i(t) + \mathbf{d}q_i^2(t) + \mathbf{e}\ell_i(t) + \mathbf{B}\mathbf{x}_i(t)\right)\mathrm{d}t + \mathbf{R}\,\mathrm{d}\mathbf{W}(t). \quad (1)$$

Here, the column vector $\mathbf{a}_i$ contains the site-specific proportional rates of change in the ilr components at the ith site, evaluated at $\mathbf{x}_i(t) = \mathbf{0}, q_i = 0, \ell_i = 0$. The vectors $\mathbf{c}$ and $\mathbf{d}$ contain the coefficients representing effects of climate at the site, $q_i(t)$, and squared climate, respectively, on each transformed component. Here, climate is the centred and scaled long-term temperature at the site, assumed to be a continuous function of time. We assume that short-term temperature fluctuations can be represented as one element of the stochastic part of the equation, as described below. We include a quadratic climate effect because it is not implausible *a priori* that some species will have nonlinear and possibly non-monotonic responses to temperature, given the 14 to 24 C range of temperatures (described below) estimated across all sites and times (and thus the same will be true of some relative proportional population growth rates). The vector $\mathbf{e}$ represents effects of centred and scaled land use at the site, $\ell_i(t)$, on each transformed component. We did not include a quadratic effect of land use because we do not have a strong *a priori* reason to believe that there will be nonlinear or non-monotonic responses of relative proportional population growth rates to land use.

The $s \times s$ matrix $\mathbf{B}$ represents the effects of $\mathbf{x}_i(t)$ on the proportional growth rate of each component. It is assumed to be the same for all sites (because to do otherwise would require large amounts of data). When $\mathbf{B} = \mathbf{0}$, each taxon follows a stochastic exponential growth model, with a growth rate dependent on changing climate and land use. This can be viewed as "a random scheme with no evidence of meaningful biological association between the various taxa" (Martin and Mosimann, 1965). In other words, $\mathbf{B} = \mathbf{0}$ corresponds to a slightly more sophisticated version of null model B from Martin and Mosimann (1965). Strictly speaking, $\mathbf{B}$ represents the effects of frequency-dependence (relative abundances) rather than density-dependence (abundances per unit area). However, there is evidence that Holocene forests were more or less closed (Mitchell, 2005), although probably somewhat more open than modern non-intervention forests (Bradshaw and Hannon, 2004). If this is the case, then total tree density would have been fairly constant over time, so that the effects of frequency- and density-dependence would have been equivalent. The noise term $\mathbf{R}\,\mathrm{d}\mathbf{W}(t)$ is white noise representing all kinds of external disturbances such as short-term temperature fluctuations, fire, storms and insects. The matrix $\mathbf{R}$ is a lower-triangular matrix with positive diagonal entries, such that the covariance of the noise term is $\mathbf{\Sigma} = \mathbf{R}\mathbf{R}^T$. Here we assume that the multivariate Wiener process $\mathbf{W}(t)$ is s-dimensional, so that $\mathbf{R}$ is $s \times s$.

The solution to Equation (1) is given in the supporting information, section S2.

2.3. Climate function

We obtained estimated temperature data from Heiri et al. (2015). These data are stacked and spliced estimates of July air temperature for the Alpine region, from multiple chironomid records, for an altitude of 1000m above sea level. We used these data to represent long-term temperature patterns for all sites (supporting information, Fig. S1), with linear interpolation between change points and altitude correction based on a temperature lapse rate of 6°C per 1000m (Heiri et al., 2015). In order to concentrate on modelling vegetation dynamics, we ignored uncertainties in these temperature values, latitude and longitude effects, and potential bias associated with using Alpine chironomid data beyond the geographical distribution of their calibration dataset (Brooks and

Langdon, 2014). Regional chironomid calibration datasets are under development (Engels et al., 2020) and could in principle be used with our approach, but as yet few have full Holocene coverage. The detailed treatment of temperature data is in the supporting information, section S3.

2.4. Human land use

We extracted data on the proportion of useable land under human use from the supporting information of Kaplan et al. (2011). We used the KK10 scenario in Kaplan et al. (2011), which assumes that land use becomes more intensive as population density increases. Land use estimates in Kaplan et al. (2011) also rely on population density data, which come from country-level graphs in McEvedy and Jones (1978), supplemented for times earlier than 3ka BP by results from a deterministic simulation model (Wirtz and Lemmen, 2003). There is substantial uncertainty in estimates of past human populations, especially at the earlier times (Cohen, 1995, p. 77). Clearly, land use estimates must also be very uncertain, but we treat them as if they were known precisely in order to simplify computation.

We matched the latitude and longitude of each site to the closest point on the 5' grid of KK10 data, and extracted proportion of human land use for this point for all available times: 8ka BP to 1850 AD, at annual intervals (Fig. 1, solid lines). The proportion of useable land under human use was strikingly higher and increased earlier for Lobsigensee (Fig. 1e) than for the other sites. There is evidence for very early agricultural activity in Switzerland (Tinner et al., 2007; Schwörer et al., 2015), and the proportion of useable land in the mountainous region around Lobsigensee is low (Kaplan et al., 2009). Thus, it is likely that early farming had substantial effects on the limited area of forest in this region, compared to fully forested lowlands. This supports our belief that the proportion of useable land under human use is an appropriate measure of human activity.

We sped up computation by using piecewise linear interpolation of land use data (supporting information, section S4). Given the substantial uncertainty discussed above, this linear interpolation is not doing major violence to the data (Fig. 1, dashed lines). In order to include pollen observations between 10ka BP and 8ka BP, we extrapolated the linear function for the earliest pair of retained land use values backwards, truncating at zero if negative values occurred (Fig. 1, dashed lines earlier than 8ka BP). This extrapolation is plausible because the land use functions from the early part of the Kaplan et al. (2011) data are almost straight lines.

2.5. Pollen observations

We used the same theoretical approach as in the REVEALS model (Sugita, 2007) to derive expected pollen proportions from the solution to Equation (1). An important feature of our approach is that we do not need to know relative pollen production, dispersal and deposition in order to study land use and temperature effects on the relative abundance of trees (supporting information, section S5). We assumed that, at a given site and time, pollen grains are sampled independently from these expected pollen proportions. In reality, the times to which these samples correspond are uncertain. In principle, this uncertainty could be incorporated into our approach, but would increase the computational difficulty. Therefore, in common with Paciorek and McLachlan (2009), we treat sample times as if they were known exactly.

We used a multinomial model for observed pollen counts, conditional on expected pollen proportions at a given time (supporting information, section S6). The multinomial arises when pollen grains are drawn from the total count in a series of independent and identical trials (Agresti, 2002, p. 6). Under this observation model, zero pollen values can occur by sampling from the set of expected pollen proportions, even for taxa with non-zero expected pollen proportions. Similar approaches have been used for proportions of space filled by sessile marine organisms, by building models for the effects of environmental factors in isometric logratio coordinates, back-transforming to obtain expected proportions, and assuming that counts of the number of randomly-chosen points at which each taxon is present are drawn from these expected proportions (Chong and Spencer, 2018; Vercelloni et al., 2020).

2.6. Simplified model

Estimation of the full model (Equation (1)) is very time-consuming unless the number of taxa is small. We therefore made two simplifying assumptions that reduce the number of parameters and speed up computation. First, we assumed that the main features of frequency-dependent interactions between logratio components can be captured by distinguishing only "self" effects (of any logratio component on itself) and "non-self" effects (of a logratio component on any other logratio component). This is similar in spirit to the assumption that most interspecific density-dependent interactions are weaker than most intraspecific density-dependent interactions (Mutshinda et al., 2009), and to common choices of a prior for the matrix corresponding to $\mathbf{B}$ in discrete-time econometric vector autoregressive models (Bańbura et al., 2010). Second, we assumed that logratio components respond independently to noise. These assumptions must not depend on the particular choice of logratio coordinates. In consequence, both the frequency-dependence matrix $\mathbf{B}$ and the noise covariance matrix $\mathbf{\Sigma}$ must be scalar multiples of the identity matrix, with parameters b_1 and σ^2 respectively (supporting information, section S7).

2.7. Parameter estimation

We used a Bayesian approach to estimation (supporting information, section S8), because state-space models such as ours are often difficult to fit using non-Bayesian methods. We used informative priors on the initial ilr coordinates $\mathbf{x}_i(0)$. We had some idea of plausible ranges of values for the difference b_1 between self- and non-self frequency-dependent effects and the site-specific intercepts $\mathbf{a}_i$, and chose priors that were very flat over these ranges. For the noise scale parameter σ^2 and the environmental effects $\mathbf{c}$,$\mathbf{d}$, $\mathbf{e}$, we had little knowledge of plausible values, but chose priors that we believed would be vague (and that were indeed very flat over the high-density region of the posterior). We fitted the model using Bayesian estimation based on the NUTS algorithm (Hoffman and Gelman, 2014) implemented in the Stan 2.16.0 programming language (Carpenter et al., 2017), with aspects of analysis done in R version 3.4.4 (R Core Team, 2018). Code is available as supporting information. We used Stan parameters and convergence checks as described in the supporting information (section S8). These checks indicated that results for Hockham Mere should be interpreted more cautiously than those for other sites.

We checked the performance of our estimation methods using a simulation study (supporting information, section S9). In summary, we generated 10 simulated data sets from the model, with the same structure as the real data and with parameter values set to their posterior mean estimates from the real data set. We determined how often the true parameter values were contained in 95% credible intervals from the simulated data. Although fitting this model is challenging, most parameters, including the temperature effects

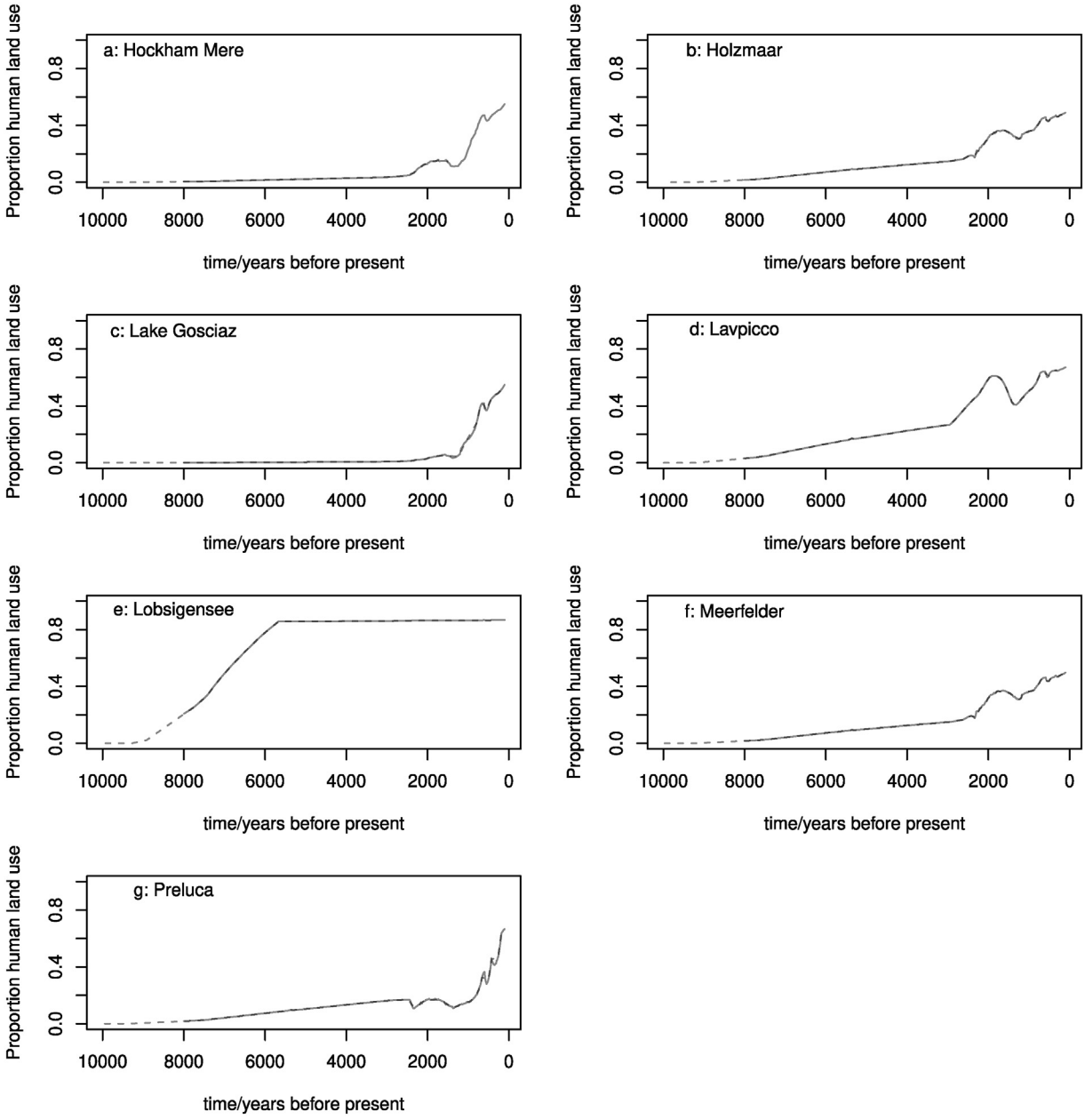

Fig. 1. Proportion of useable land under human use against time for each site. Data extracted from Kaplan et al. (2011). Solid line: original data. Dashed line: extrapolated back to first pollen observation, and linear interpolation between pollen observation times.

c and **d** and the land use effect **e**, which are our main focus, appeared to be well estimated. There was evidence of substantial small-sample bias in estimation of the self-versus non-self frequency-dependent effect parameter b_1 (supporting information, section S9), but this does not affect our main results. We checked the extent to which it is possible to separate climate and land use effects by plotting the posterior pairwise relationships between components of the linear (**c**) and quadratic (**d**) climate effects and the land use effect (**e**): we discuss these relationships in the results section.

We checked the plausibility of the model using graphical posterior predictive checks. We sampled parameters from their posterior distributions, and then simulated trajectories of sample pollen proportions for each site and taxon, including the effects of environmental variables and noise, with the same numbers of pollen grains at each observation time as the real data. We plotted the simulated trajectories, and compared them visually with the observed trajectories.

2.8. Comparing effects of land use and temperature

We measured the instantaneous effects of changes in land use and temperature on individual taxa by taking the derivatives of the deterministic part of the rate of change with respect to land use and temperature respectively, and back-transforming to centred log-ratio coordinates (supporting information, section S10). This gives the effect of changes in land use or temperature on the proportional population growth rate of each taxon, relative to the mean proportional population growth rate for all taxa. These quantities can be thought of as effects on the mean rate of competitive exclusion

(Pásztor et al., 2016, p. 122) of all taxa of interest by a given taxon *i*. These estimates of land use and temperature effects are comparable, because we scaled both land use and temperature by their standard deviations. However, the value of the derivative for land use is a constant, while that for temperature is a linear function of temperature, because we assumed linear and quadratic effects of land use and temperature respectively (Equation (1)).

We obtained rough visual estimates of how human land use and temperature may have affected forests at each site over most of the last 10ka by calculating posterior distributions of expected pollen proportions under four scenarios: observed land use and temperature; land use set to its initial value (zero for all sites) but observed temperature; observed land use but temperature set to the mean for each site; and land use set to its initial value and temperature set to the mean for each site. Zero land use is the natural reference point, because we are interested in how forests might have developed in the absence of growth in human land use. To study dynamics in the absence of temperature change, some constant temperature must be chosen. We chose the mean temperature for each site. We feel that this is a more natural reference point than the temperature at 10ka BP because in contrast to land use, there is no particular interest in the temperature at the start of the time series. However, other choices could have been made. Note that there will still be differences in dynamics among sites due to temperature, because temperature affects different taxa in different ways, and mean temperature differs among sites. Although the visual estimates from this approach are convenient and easy to understand, they are rough, because expected relative abundances depend on b_1, for which we know estimation was biased.

We therefore developed a more rigorous way to compare the magnitudes of land use and temperature effects on the rate of change of forest composition. For each site and pollen observation time, we calculated the rate of divergence in expected relative abundances between a forest with the observed land use and temperature and one with zero human land use but observed temperature. Similarly, we calculated the rate of divergence between a forest with observed land use and temperature and one with observed land use but mean temperature. The difference Δ between these two rates tells us about the importance of land use compared to that of temperature, with positive values meaning that land use is having a larger effect, and negative values that temperature is having a larger effect. This difference can be estimated reliably, because the only parameters on which it depends are $\mathbf{c}$, $\mathbf{d}$ and $\mathbf{e}$, all of which we can estimate well (supporting information, section S11). In addition, Δ tells us about the overall size of the effects of land use and temperature, because it measures the effect of given values of these variables, rather than just the sensitivity of the rate of change to small changes in them. Lastly, Δ tells us about effects at a particular time, because it is based on rates of change, in contrast to differences in expected composition, which are the outcome of effects integrated over time.

3. Results

Human land use increased earlier and reached a higher level at Lobsigensee (Fig. 1e) than at the other sites. The results for Lobsigensee also highlight the strengths and weaknesses of the model. We therefore concentrate on Lobsigensee in the main text, but present results for all sites in the supporting information (Figs. S22–S56).

There were substantial changes in sample pollen proportions over time at Lobsigensee (Fig. 2, dots). *Corylus* was initially dominant, but declined over time (Fig. 2c, although there was a short-lived peak at about 2ka BP). *Ulmus* and *Quercus* (Fig. 2j and h) were also present initially in non-negligible proportions. There were early increases followed by declines in *Fraxinus*, *Tilia* and *Ulmus* (Fig. 2e, i and j, although *Fraxinus* also had a short-lived peak at about 2ka BP). There were late increases in *Picea* and *Pinus* (Fig. 2f and g). *Alnus*, *Betula*, *Fagus* and *Quercus* appeared to oscillate (Fig. 2a, b, d and h). At all sites, estimates of expected pollen proportions (the underlying proportions of each pollen type, from which observations are sampled) tracked the sample pollen proportions very closely (supporting information, Figs. S22–S28).

Expected pollen proportions captured many of the overall trends reasonably well at Lobsigensee (Fig. 2, green lines and 95% credible bands), although the observed late increases in *Picea* and *Pinus* (Fig. 2f and g) were not captured, and the expected increase in *Fagus* was later and more gradual than observed (Fig. 2d). However, the observed oscillations in *Alnus*, *Betula*, *Fagus* and *Quercus* did not appear in the expected pollen proportions (Fig. 2a, b, d and h). The expected pollen proportions are smooth functions of time except at change points in the environmental variables (supporting information, Equation S5), and reflect the predictable, deterministic features of the model. The credible bands indicate the consequences of parameter uncertainty. However, individual trajectories from the model are affected by noise, and are thus not smooth. The model appears to treat the oscillations in *Alnus*, *Betula*, *Fagus* and *Quercus* as being due to noise rather than deterministic (a point to which we return in the discussion). Perhaps as a consequence of this, in posterior predictive checks, where we simulated multiple trajectories from the model (incorporating the effects of noise), they generally showed greater short-term variability than the real data (supporting information, Figs. S50–S56).

Although each site had idiosyncratic temporal dynamics, there were some common features of model performance. In particular, the expected increase in *Fagus* from the model was later than observed at Holzmaar (supporting information, Fig. S30d), Lavpicco (supporting information, Fig. S32d), Meerfelder (supporting information, Fig. S34d) and Preluca (supporting information, Fig. S35d). At Meerfelder and Preluca, there were substantial differences between expected and sample pollen proportions for some other taxa (supporting information, Figs. S34 and S35). As for Lobsigensee, the model appears to treat these as noise.

Increases in human land use were estimated to have positive effects on proportional population growth rates of *Fagus* and *Picea*, and negative effects on *Tilia* and *Ulmus*, relative to the mean for all taxa (Fig. 3). For other taxa, the 95% credible intervals included zero, and so we cannot draw clear conclusions about the direction of land use effects. These effects were estimated across all sites based on the shared land use effect parameter $\mathbf{e}$. However, the consequences for expected pollen proportions differed among sites, because pollen proportions were also affected by site-specific intercepts $\mathbf{a}$ and initial relative abundances $\mathbf{x}_0$. As noted in the methods, results about expected pollen proportions are rough because they depend on the parameter b_1, for which estimation is biased, but are likely to give a qualitative guide to land use effects. If human land use at Lobsigensee had remained at its initial value of zero, there would have been more *Tilia* and *Ulmus*, slightly more *Fraxinus* and *Pinus*, and less *Alnus*, *Betula*, *Fagus* and *Picea* than under the pattern of land use change that actually occurred (Fig. 2, orange dashed lines and 95% credible bands). Holding land use at zero was predicted to have little effect at Hockham Mere (supporting information, Fig. S29) and Lake Gościaż (supporting information, Fig. S31). At the other sites, holding land use at zero often resulted in more *Tilia* and *Ulmus* and less *Alnus* and *Fagus* than under observed patterns of land use change (supporting information, Figs. S30, S32, S34 and S35), although the effects were weaker than at Lobsigensee. Reductions in *Picea* were less apparent, because Preluca was the only

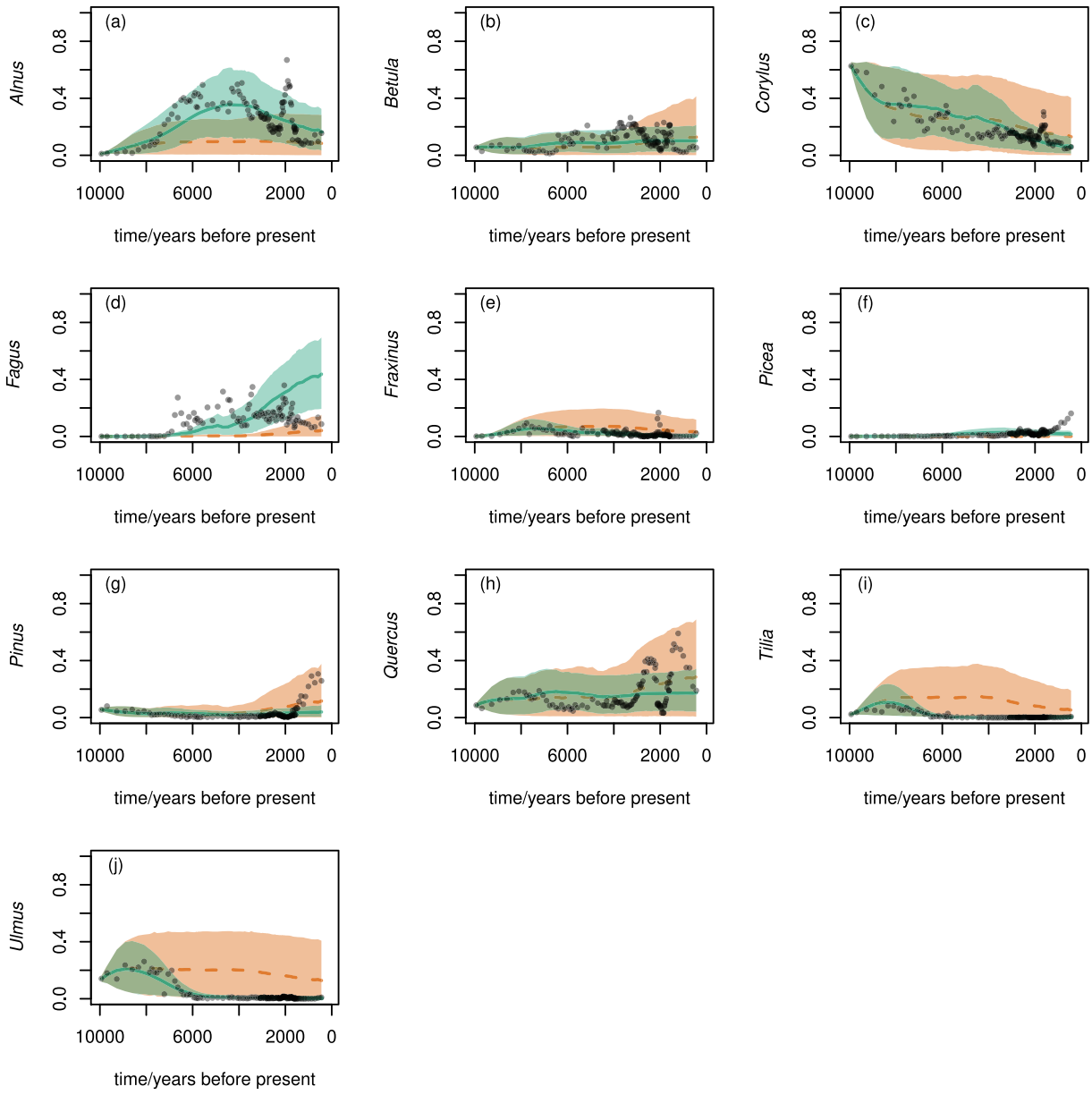

Fig. 2. Lobsigensee, expected relative abundances of pollen from each of 10 tree taxa, in the absence of noise. Solid green line and green band: posterior mean and 95% highest posterior density credible band. Black dots: sample pollen proportions. Dashed orange line and orange band: posterior mean and 95% highest posterior density credible band with land use held at its initial value. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

site other than Lobsigensee at which *Picea* was observed in a non-negligible proportion (supporting information, Fig. S35f).

Increases in temperature were estimated to have negative effects on the proportional population growth rate of *Fagus* relative to the mean for all taxa, especially at higher temperatures (Fig. 4d). For all other taxa, the 95% credible band for temperature effects included or almost included zero for almost all temperatures (Fig. 4). The effects on expected pollen proportions of holding temperature at the mean for each site, with or without holding land use at its initial value, were broadly consistent across most sites, with the exception of Hockham Mere and Lake Gościaż. However, these effects were subject to high uncertainty, and as above, we have only rough estimates. At Lobsigensee, holding temperature at its mean resulted in more *Corylus* and less *Fagus* and *Quercus* (Fig. 5, blue dashed lines and 95% credible bands). This pattern was fairly consistent across most other sites, with the exception of Hockham Mere, at which all effects were small, and Lake Gościaż, at which holding temperature at its mean tended to lead to more rather than less *Quercus* (supporting information, Figs. S36 to S42). When land use was held at its initial value and temperature was held at its mean, there were increases at Lobsigensee in *Corylus*, *Fraxinus*, *Tilia* and *Ulmus*, and decreases in *Alnus*, *Betula*, *Fagus* and *Quercus*, and there was little change in expected pollen proportions after about 6ka BP (Fig. 6, pink dashed lines and 95% credible bands). Effects at other sites were broadly similar, with the exception of Hockham Mere, where all effects were small, and Lake Gościaż, where *Quercus* tended to increase rather than decrease (supporting information, Figs. S43 to S49).

There was some difficulty in separating the effects of climate from those of land use. There were moderately strong positive relationships between components of the linear climate effect **c** and the corresponding components of the land use effect **e**, as indicated

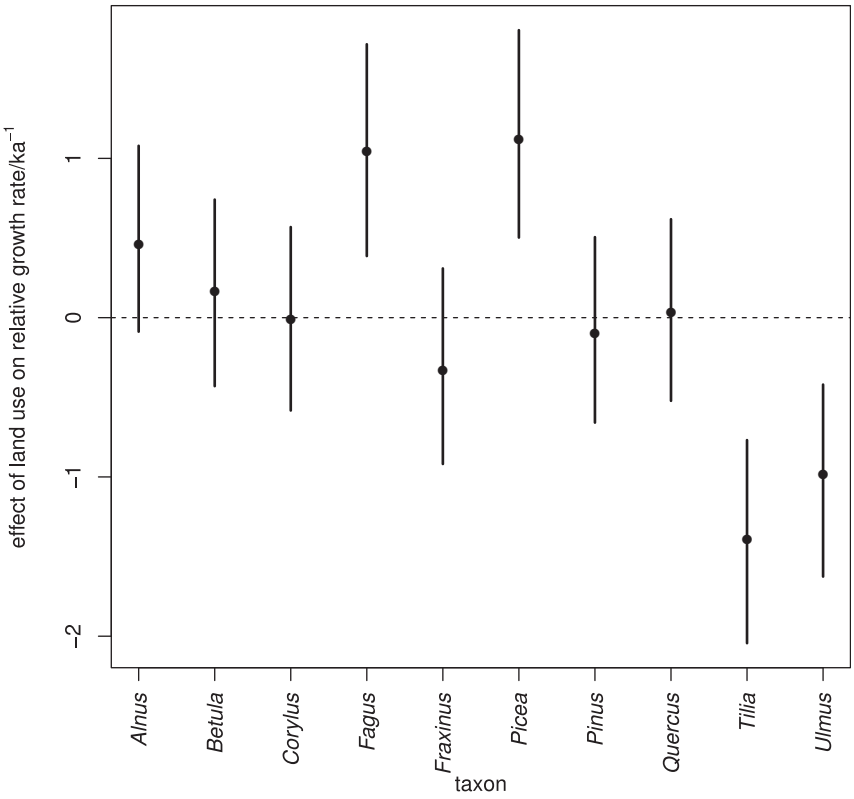

Fig. 3. Effects of a unit change in centred and scaled proportion of useable land under human land use on proportional population growth rate for each taxon, relative to the mean for all taxa. Dots are posterior means, and lines are 95% highest posterior density credible intervals. Dashed line indicates no effect.

by their posterior distributions (supporting information, Fig. S57), although little evidence of relationships between components of the quadratic climate effect **d** and the land use effect (supporting information, Fig. S58). The positive relationship between corresponding components of **c** and **e** indicates that increases in long-term temperature and increases in land use tend to act in the same direction. In the observations, temperature tended to decrease over time (supporting information, Fig. S1), while land use tended to increase over time (Fig. 1). Thus, to explain a given pattern of change in proportional population growth rates over time, if the estimated linear effect of climate is large, the estimated effect of land use must be large to offset it. Nevertheless, the relationship between climate and land use effects was not so strong that they cannot be distinguished at all.

At all sites other than Lobsigensee, temperature had larger effects than land use on the rate of change of forest composition (Fig. 7). At Lobsigensee, the effect of land use was larger than that of temperature between about 7ka and 4ka BP (Fig. 7). The value of Δ at a given time depends on how far land use is from zero, and how far temperature is from the mean for the site. During the time interval from 7ka to 4ka BP, human land use at Lobsigensee was very high (Fig. 1e), but the later decline in temperature (Fig. S1) had not yet begun.

4. Discussion

Our model allowed us to disentangle the effects of human land use and temperature on European central-latitude forests during the Holocene. We showed that relative proportional population growth rates of *Fagus* and *Picea* were positively affected by intensified human land use, while *Tilia* and *Ulmus* were negatively affected. We also showed that above about 18 °C, the relative proportional population growth rate of *Fagus* was negatively affected by increases in temperature. Overall, the effects of temperature on the rate of change of forest composition were more important than those of land use. The compositional data analysis approach that we used has a natural ecological interpretation in terms of relative population growth rates, and does not require information on pollen production, dispersal, or deposition. As we outline below, there are still areas in which both technical improvements and theoretical advances are needed. There were short-term oscillations that were not well described, perhaps because of either lack of local detail in land use data or over-simplification of our model. Our model also had difficulty with late increases in taxa such as *Fagus*, *Picea* and *Pinus*, perhaps because we did not include processes such as dispersal, modern silviculture and fire. Nevertheless, our models captured most of the overall trends at seven European central-latitude sites, and led to estimates of land use effects that are consistent with current thinking.

Our results relied on several methodological innovations. We developed a continuous-time stochastic model for forest composition, with a multinomial observation model for pollen counts. This model is broadly applicable to pollen count data and is ecologically meaningful. Continuous time is appropriate because pollen counts are often unequally spaced. Furthermore, continuous-time models can often be interpreted as systems of causal relationships, whose parameters provide information on the rates of underlying ecological processes such as competition and environmental effects on population growth. In contrast, the parameters of a discrete-time model for an underlying continuous-time system describe the outcome of multiple processes, and can be difficult to interpret (Harvey, 1990, p. 503). The closest existing models to ours were developed by Jeffers et al. (e.g. 2015). Their approach is statistical and is founded on standard ecological

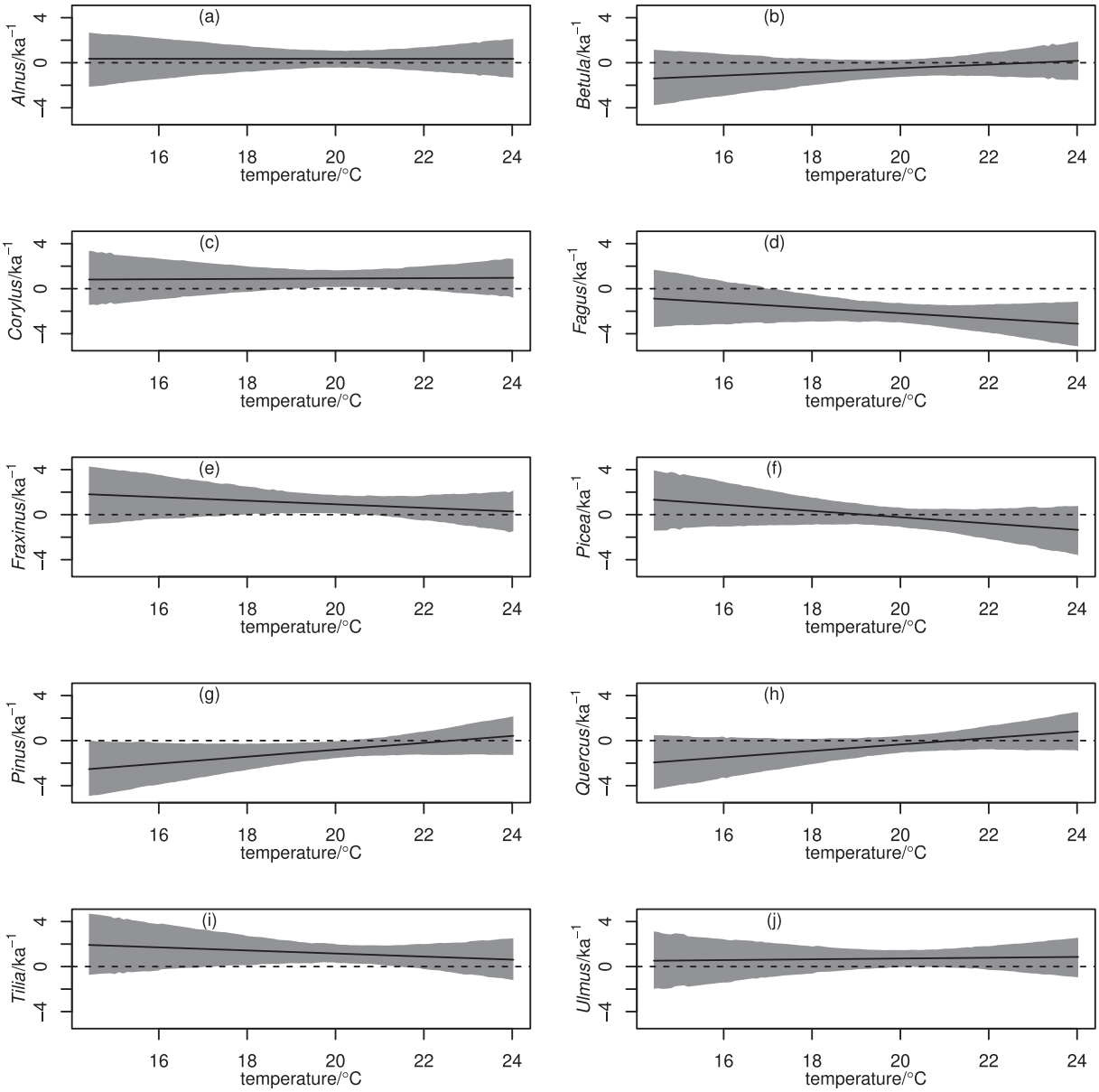

Fig. 4. Effects of a unit change in centred and scaled temperature on proportional population growth rate for each taxon, relative to the mean for all taxa. Solid lines are posterior means, and grey bands are 95% highest posterior density credible bands. Dashed line indicates no effect.

models for interspecific interactions. However, their models describe pollen accumulation rates (as a proxy for biomass) rather than pollen counts, and therefore do not require the algebraic framework of compositional data analysis (and also do not fully account for unequal observation intervals, the nonlinearity in the process they assumed, or observation error). Compositional data analysis is a natural choice for pollen count data, which usually provide only relative information. Furthermore, we showed (supporting information, section S5) that with the compositional framework and the theory underlying the REVEALS model (Sugita, 2007), environmental effects on tree relative abundances can be studied without knowing pollen production, dispersal and deposition. Compositional data analysis also simplifies the analysis of changes in community composition over time (Gross and Edmunds, 2015), on environmental gradients (Chong and Spencer, 2018) and in response to experimental manipulation (Billheimer et al., 2001), and leads to a measure of rate of change with a natural interpretation. The obvious compositional measure of rate of change (Spencer, 2015) is the mean over pairs of taxa of the standard measure of the rate of competitive exclusion (Pásztor et al., 2016, p. 122). In contrast, other measures of rate of change popular in palaeoecology, such as those based on detrended correspondence analysis (e.g. Jacobson and Grimm, 1986) and on Hill numbers other than the total number of species present (e.g. Felde et al., 2018), have no natural interpretation in terms of population dynamics, and have the undesirable property that they are not constant even when the abundance of every taxon is changing at a constant proportional rate (Spencer, 2015). Overall, our statistical approach complements dynamic global vegetation models such as LPJ-GUESS (Smith et al., 2001) by using time series data to estimate parameters, and by being formulated at the population rather than the physiological level, but remains rooted in ecological theory.

Despite this theoretical foundation, some issues with our approach remain unresolved, and may be productive directions for

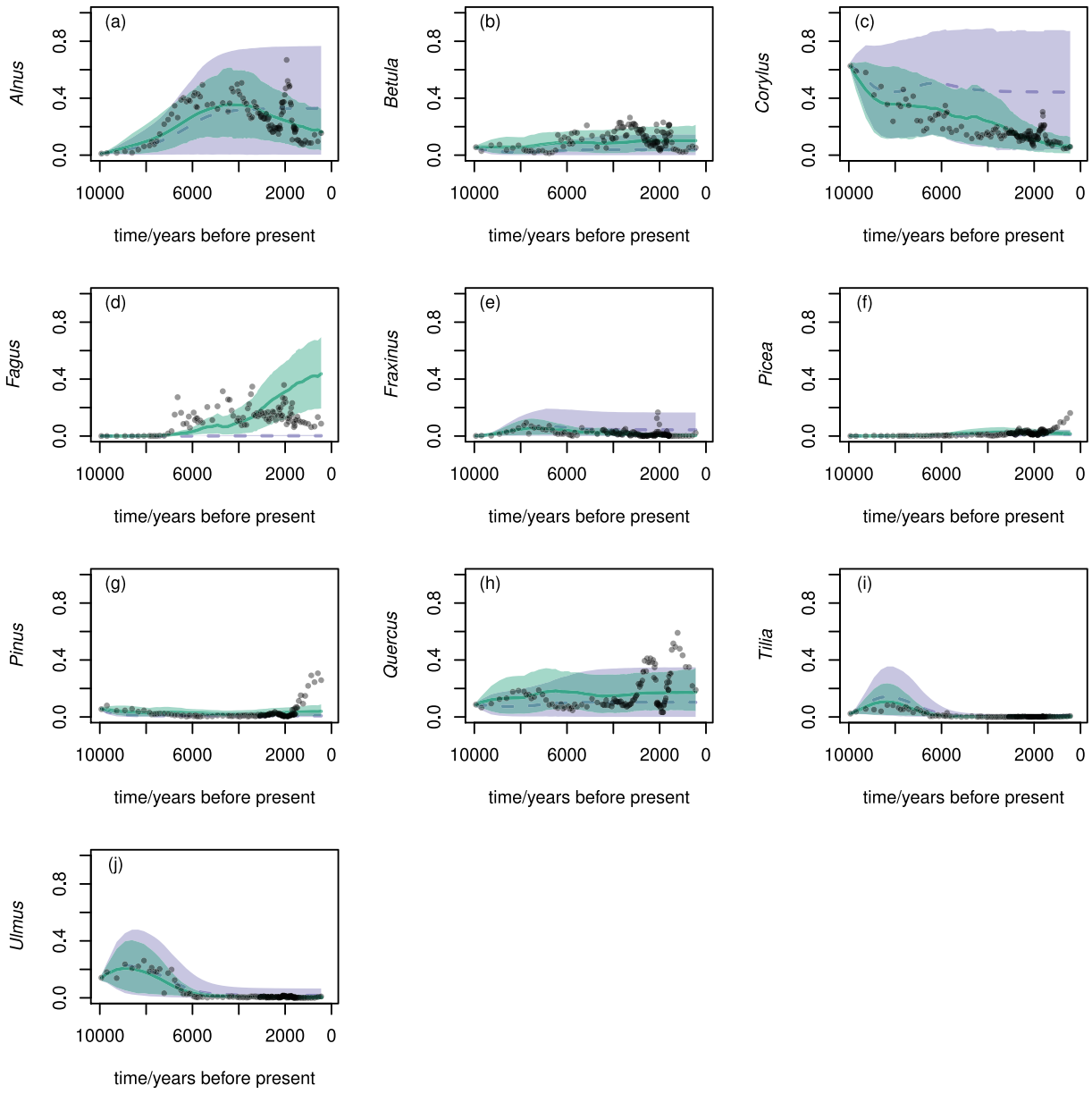

Fig. 5. Lobsigensee, expected relative abundances of pollen from each of 10 tree taxa, in the absence of noise. Solid green line and green band: posterior mean and 95% highest posterior density credible band. Black dots: sample pollen proportions. Dashed blue line and blue band: posterior mean and 95% highest posterior density credible band with temperature held at its mean value for the site. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

future work. For example, our model treated the apparent oscillations in composition at Lobsigensee (Fig. 2) as stochastic. It has been suggested that these oscillations were driven by fluctuations in the intensity of human land use (Rey et al., 2019) that were not captured in our land use data. Endogenous oscillations are also possible in principle, but the simplified model we fitted cannot generate endogenous oscillations. A model with an unconstrained frequency dependence matrix **B** could generate such oscillations, although at the cost of identifiability issues for regularly-spaced observations (Phillips, 1973). Nonlinear models can also generate endogenous oscillations. More work is needed on nonlinear models that are appropriate for ecological compositional data. Early results indicate some interesting problems. For example, both the exponential and logistic models are special cases of the same linear compositional model, while the addition of immigration leads to a nonlinear compositional model (Pawlowsky-Glahn et al., 2015, chapter 9). The biggest computational issue is dealing with larger numbers of taxa, especially if they come from a wider range of plant functional types. The simplifying assumption that it is only necessary to distinguish between "self" and "non-self" interactions becomes much less appropriate when very different taxa are modelled. There may nevertheless be possible simplifications. For example, assuming that a small number of latent factors drive dynamics has been a successful approach in discrete-time models of econometric (e.g. Stock and Watson, 2002) and ecological (Ovaskainen et al., 2017) systems. If the latent factors are linear combinations of log abundances (Ovaskainen et al., 2017), constraining the weights to sum to zero across taxa makes each factor into a logcontrast (Aitchison, 1986, p. 84). Logcontrasts can represent properties of a composition such as the log of the ratio of abundances of one type of plant to another (such as forest versus non-forest plants), and so identifying a small number of

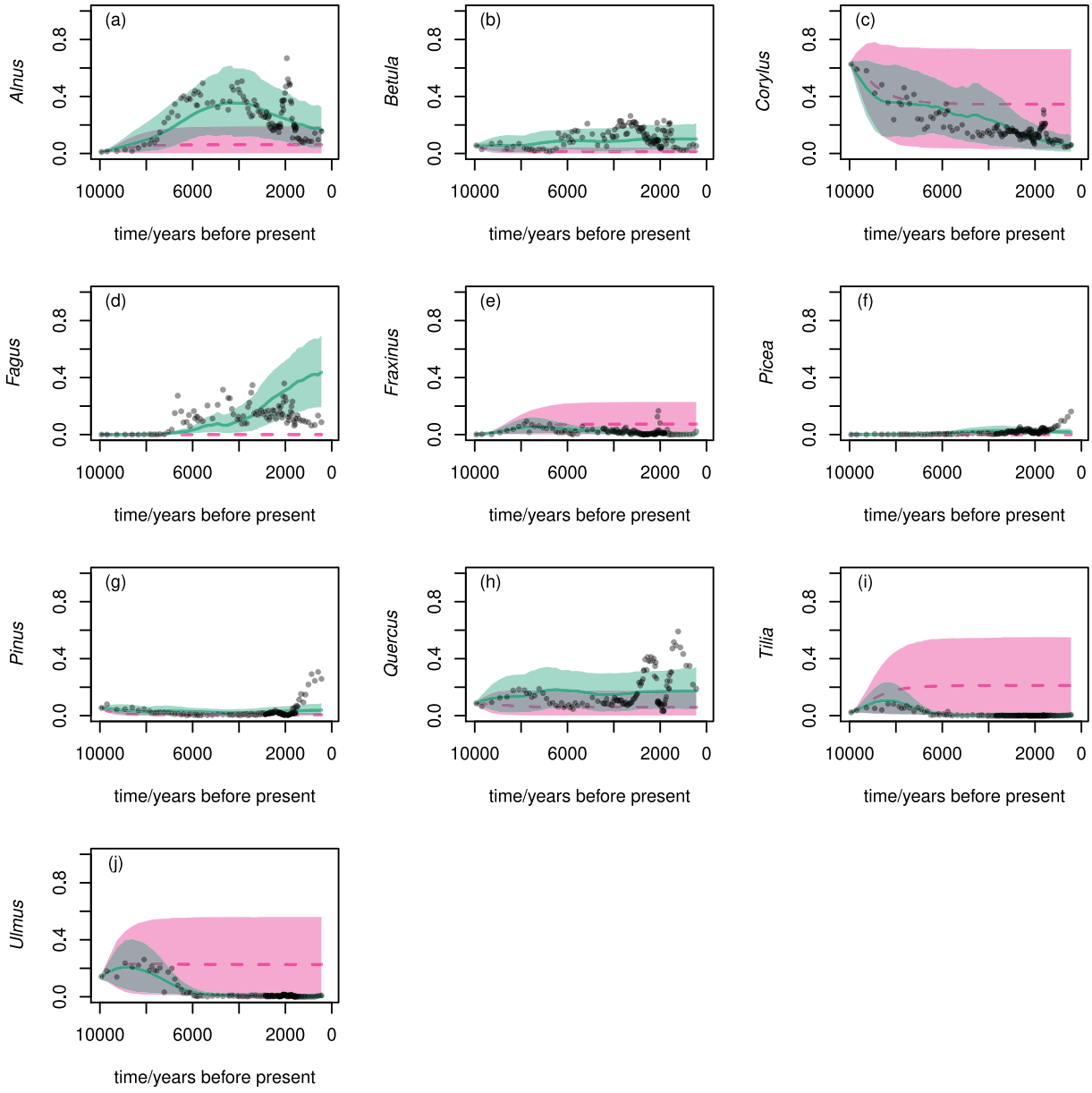

Fig. 6. Lobsigensee, expected relative abundances of pollen from each of 10 tree taxa, in the absence of noise. Solid green line and green band: posterior mean and 95% highest posterior density credible band. Black dots: sample pollen proportions. Dashed pink line and pink band: posterior mean and 95% highest posterior density credible band with land use held at its initial value and temperature held at its mean value for the site. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

logcontrasts that drive dynamics could be very informative. However, it is easy to construct ecosystem models in which logcontrasts are not sufficient to describe dynamics (Boit and Spencer, 2019), and more remains to be done on ecologically meaningful dimension reduction for dynamics.

The approach adopted here generates modelled pollen proportions that capture many of the overall trends in the pollen data from Lobsigensee (Fig. 2). The overall correspondence between changes in pollen proportions and the modelled dynamics is an improvement on a similar comparison using output from the dynamic vegetation model LPJ-GUESS and pollen accumulation rate data from sites in Scandinavia (Miller et al., 2008). The earlier study did not include a human impact dataset and the modelled climatic data were 1ka mean values, so the inclusion of land use and the higher resolution summer temperature estimates have likely contributed to improved accuracy of the modelled outputs. Both studies had difficulties with recent abundance dynamics of *Picea* and *Pinus*, suggesting that factors such as modern silviculture and altered fire regimes, which are not explicitly accounted for in the models, are significant determinants of modern forest composition.

Our analyses allowed us to estimate the effects of changes in land use and temperature on relative proportional population growth rates of taxa. The positive effects of intensified land use on *Fagus* and *Picea*, and negative effects on *Tilia* and *Ulmus* (Fig. 3), provide independent support for prior suggestions made in the literature. For example, Giesecke et al. (2017) identified two types of change most likely influenced by human activities. Firstly, sustained population increases for *Fagus* in northern and central Europe that were mediated by anthropogenic disturbance (Giesecke et al., 2007), because *Fagus* establishes well on

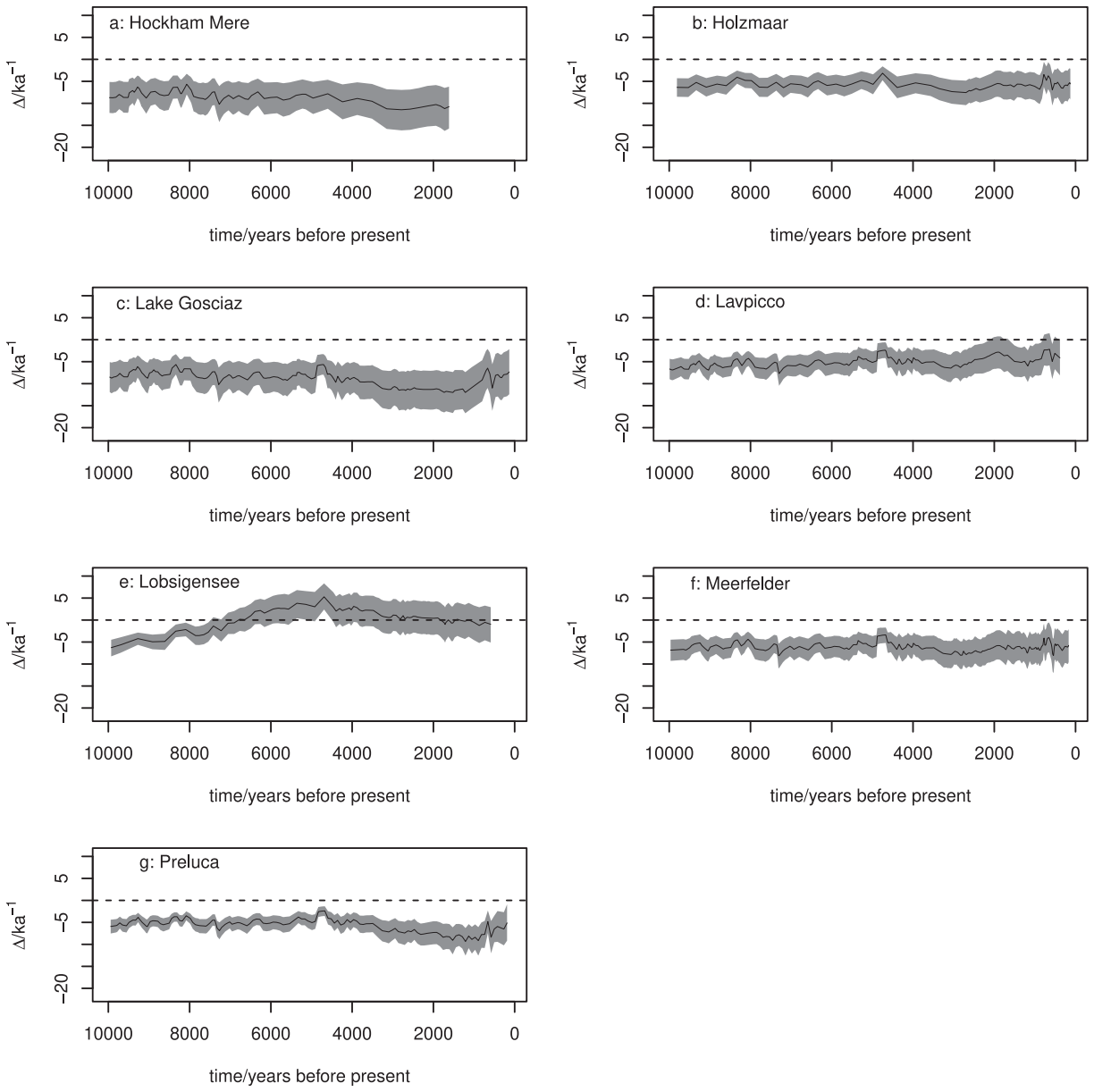

Fig. 7. Comparison of magnitudes of land use and temperature effects on the rate of change of forest composition, for each site and pollen observation time. Solid lines are Δ (in ka^{-1}), the difference in rate of divergence due to land use and temperature effects, with positive values indicating that land use has the greater effect, and negative values that temperature has the greater effect. Grey bands: 95% highest posterior density credible bands. Dashed horizontal line: $\Delta = 0$, indicating equal importance of land use and temperature.

abandoned field sites (Odgaard, 1994). Secondly, declines in abundance that were not necessarily linked to range contractions, best demonstrated for *Tilia* populations reduced by forest clearance for agriculture (Turner, 1962; Grant et al., 2011). Relative proportional population growth rates of *Fagus* were reduced by mean July temperatures above 18°C in our analysis (Fig. 4d), and previous work has shown *Fagus* to be most abundant at a mean July temperature of 18°C (Huntley and Webb, 1989). The influence of temperature on Holocene *Picea* population dynamics in Europe has been widely discussed (Bradshaw et al., 2000). However, we did not see clear effects of changes in temperature on relative proportional population growth rates for *Picea* (Fig. 4f), perhaps because *Picea* was rare at most of our sites (and absent at Hockham Mere).

Over the entire Holocene, temperature had larger effects than land use on the rate of change of forest composition at all sites except Lobsigensee (Fig. 7), where land use was particularly intensive during certain time intervals in the Neolithic and Bronze Age (Hafner et al., 2014). There was some evidence of slight increases in the importance of land use during the last two millennia at other sites, but temperature nevertheless remained more important. Human impact on land cover has chiefly been the replacement of forest by agricultural land (Roberts et al., 2018), while we are considering only changes in tree composition within forests. It is likely that the importance of land use would be greater if forest clearance was considered. Thus, including more taxa from a wider range of land cover types (e.g. Trondman et al., 2015) should be a priority for broader assessment of the effects of land use. Nevertheless, our study of the major forest trees indicates that human impact within the remaining forests was chiefly subordinate to the effects of temperature. We use no data from the last

100a BP, and so miss much of the impact of the rise of commercial forestry and altered forest composition due to heavy browsing pressure and other management issues that were chiefly confined to recent centuries (Naudts et al., 2016). Our results are generally consistent with Marquer et al. (2017), who found that climate explained a larger fraction than human land use of the spatio-temporal variation in Holocene vegetation in Europe. In their approach, based on redundancy analysis, the underlying ecological theory is static and assumes that species distributions are determined directly by the environment (Legendre and Legendre, 2012, p. 699). It is reassuring that such a different set of assumptions leads to conclusions broadly consistent with ours.

In conclusion, we have developed an approach to modelling forest composition over long time periods which is broadly applicable and is founded on ecological principles. Using this approach, we have shown that the effects of temperature outweigh those of human land use in European central-latitude forests, even during recent millennia.

Author statement

Gregg Milligan: Conceptualization, Methodology, Software, writing. Richard Bradshaw: Conceptualization, Methodology, Resources, writing. Damian Clancy: Conceptualization, Methodology, Formal analysis, writing. Kamila Zychaluk: Conceptualization, Methodology, Formal analysis, writing. Matthew Spencer: Conceptualization, Methodology, Software, Formal analysis, writing.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.quascirev.2020.106458.

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